

Substrate Selection by Fantail (*Etheostoma flabellare*), Greenside (*E. blennioides*), and Rainbow (*E. caeruleum*) Darters¹

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ABSTRACT. The seasonal substrate preferences of fantail, greenside, and rainbow darters were examined in a laboratory stream tank. The fantail darter, tested singly or in the presence of congeners, exhibited a strong preference for the largest substrates (i.e., pebble, cobble-boulder) in all seasons. The percentage of observations of fantail darters on pebble and cobble-boulder substrates ranged from 44.3% to 71.1%. Of the three species examined, the greenside darter showed the greatest preference for the largest substrates. The percentage of observations on the pebble and cobble-boulder substrates for this species ranged from 52.1% to 73.9%. In contrast to the other species, the rainbow darter used all substrates with approximately equal frequency. The results of similarity analyses revealed high levels of overlap (>0.600) in substrate use among the three species in all seasons. However, interspecific differences in morphology, foraging method, and foraging area may reduce the potential for competition for space among these species.

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INTRODUCTION

The composition and arrangement of available substrates are major determinants of the distributions and habitat preferences of benthic organisms. Although the importance of substrate type in governing habitat selection, species distributions, and species densities has been demonstrated for bottom-dwelling stream insects (e.g., Allan 1975, Brown and Brown 1984), studies of fishes have not been as conclusive. Many stream fishes are not closely associated with substrate, and use the stream habitat in a three-dimensional fashion. For instance, Baker and Ross (1981), Surat et al. (1982), and Mendelson (1975) analyzed habitat selection and partitioning in shiner (*Notropis* spp.) species assemblages, and found that the position of the fish in the water column was the major axis along which habitat partitioning occurred. Substrate type in these communities was of relatively low importance in habitat selection.

The distributions of bottom-dwelling fishes are more likely to be strongly influenced by substrate composition and heterogeneity. Curry and Spacie (1984) reported that catostomids partitioned spring spawning areas primarily on the basis of the distribution of substrate sizes. Matheson and Brooks (1983) found that the mottled sculpin (*Cottus bairdi*) and the Potomac sculpin (*C. girardi*) partitioned the stream habitat by substrate type. Bottom-dwelling darters of the genus *Etheostoma* (Pisces: Percidae) may also show distributions that are strongly influenced by substrate composition. It is not uncommon to find several species of *Etheostoma* occurring sympatrically in the riffles of a stream. With the high degree of substrate patchiness and heterogeneity present in riffles (Hynes 1970), differences in substrate preference among darters may lead to partitioning of the riffle habitat and result in reduced competitive pressure. Page (1983) noted that substrate composition probably restricts the distributions of darters in streams, and that substrate use is strongly linked to the morphology of each species in this group. Page and Swafford (1984) discussed the importance of morphological adaptations in darters to the ecological specializations observed in these forms.

The objectives of the present study were to: 1) examine the seasonal substrate preferences of fantail (*Etheostoma flabellare*), rainbow (*E. caeruleum*), and greenside (*E. blennioides*) darters; 2) measure the effects of interspecific interactions on these preferences; and 3) relate substrate preferences to the habitat partitioning observed by other investigators.

MATERIALS AND METHODS

Adult fantail, rainbow, and greenside darters were collected in summer (August), autumn (October), winter (December), and spring (April), 1984-1985, from Indian and Lost Creeks in southwestern Ohio (site descriptions in Hlohowskyj and Wissing 1985). Fish were returned to the laboratory, held for one week at room temperature (18-22 C) in 20-liter glass aquaria provided with constant aeration, and fed frozen brine shrimp on alternate days.

All substrate selection tests were conducted in a U-shaped stream tank (Frigid Units Inc., Toledo, Ohio). The tank was divided into four identical chambers, each 216 cm long \times 34 cm wide (Fig. 1). Water depth was 25 cm and current velocity was zero. The chambers were separated with vinyl window screening (2-mm mesh). Substrate classes used for the selection tests were modified from Cummins (1962) and consisted of sand (<0.5 mm diam.), fine gravel (0.6-3.0 mm diam.), medium gravel (3.0-6.0 mm diam.), coarse gravel (6.0-16.0 mm diam.), pebble (16-64 mm diam.), and cobble-boulder (>64 mm diam.). The substrates in each test chamber were arranged linearly in the following order: sand, fine gravel, medium gravel, coarse gravel, pebbles, and cobbles-boulders. Each section of substrate was approximately 36 cm in length (Fig. 1).

To determine substrate preferences, six adult fantail (mean standard length \pm standard deviation, mm: 51.4 ± 4.3), rainbow (43.9 ± 4.1), and greenside (60.4 ± 5.1) darters were placed in the first, second, and third test chambers, respectively. The fourth test chamber received six individuals of each species. After the chambers were covered with vinyl window screening, the fish were left undisturbed for a period of four days. During this time, the fish were exposed to a 12:12LD photoperiod and were not fed. Water temperatures in the test chambers ranged from 18 to 22 C.

Substrate preferences were determined by observing darter locations within the chambers at 0730, 1200, 1900, and 2330 hrs (EST) for a period of four days and recording the substrates occupied by the fish. All tests were then repeated with new fish. To determine the effects of the testing chamber on darter distribution, control tests were conducted with fish in the chambers in the absence of substrates. Differences among control, single-species, and mixed-species distributions were compared by Chi-square analysis (Sokal and Rohlf 1981). All significance levels were set at $P < 0.05$.

Schoener's (1968) index of similarity (D) was employed to measure the degree of similarity in substrate class use between species. The index is calculated as:

$$D = 1 - 1/2 \sum_{i=1}^n |P_{Ai} - P_{Bi}|$$

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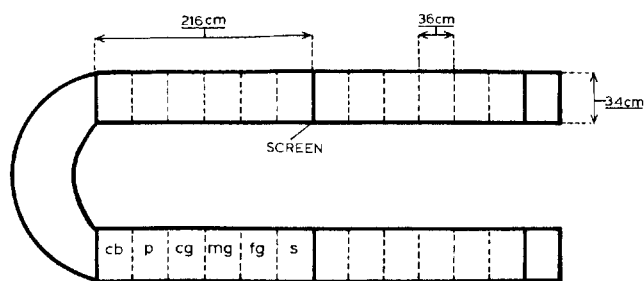


FIGURE 1. Schematic diagram of the substrate preference test chambers. Substrate classes: s, sand (<0.5 mm dia.); fg, fine gravel (0.5-3.0 mm dia.); mg, medium gravel (3.0-6.0 mm dia.); cg, coarse gravel (6.0-16.0 mm dia.); p, pebble (16.0-64.0 mm dia.); cb, cobble-boulder (>64 mm dia.).

where:

i = the i th substrate class,

P_{Ai} = the percentage of observations of species A in the i th substrate class, and

P_{Bi} = the percentage of observations of species B in the i th substrate class.

Values for D range from 0.000 (i.e., the two species are using completely different substrate classes) to 1.000 (i.e., identical substrate use by the two species).

RESULTS

Typical distributions of the darters in the absence of substrates (control distributions) are shown in Figure 2. The three species exhibited strong preferences for the ends of the chambers in all seasons except for rainbow darters in summer. In summer, this species was approximately evenly distributed throughout the tank. The end-effect exhibited by the three species probably resulted from the fish attempting to seek cover in the corners of the chambers.

The fantail darter exhibited distributions within the substrates that were significantly different ($P < 0.05$) in all seasons from the control distributions. This species also showed a strong preference for the largest substrate particles in all seasons (Fig. 3). The percentage of observations on pebble and cobble-boulder substrates for the fantail darter ranged from 44.3% in autumn to 71.1% in winter. There was no difference in distribution on the substrates between summer and autumn or summer and winter ($P > 0.05$).

The distributions of fantail darters in the presence of rainbow and greenside darters were significantly different ($P < 0.05$) from the controls in all seasons (Fig. 3). Distributions also differed seasonally except between summer and winter and summer and spring. The percentage of observations of fantail darters on the largest substrates ranged from 59.4% (spring) to 65.5% (winter). Although significant differences among the single- and mixed-species tests were found in all seasons, the overall distributions of the fish were not markedly different (Fig. 3).

Of the three species tested, the greenside darter showed the greatest preference for the largest substrates. The percentage of observations on the pebble and cobble-boulder substrate classes ranged from 63.9% in winter to 73.9% in spring for this species (Fig. 4). The frequency

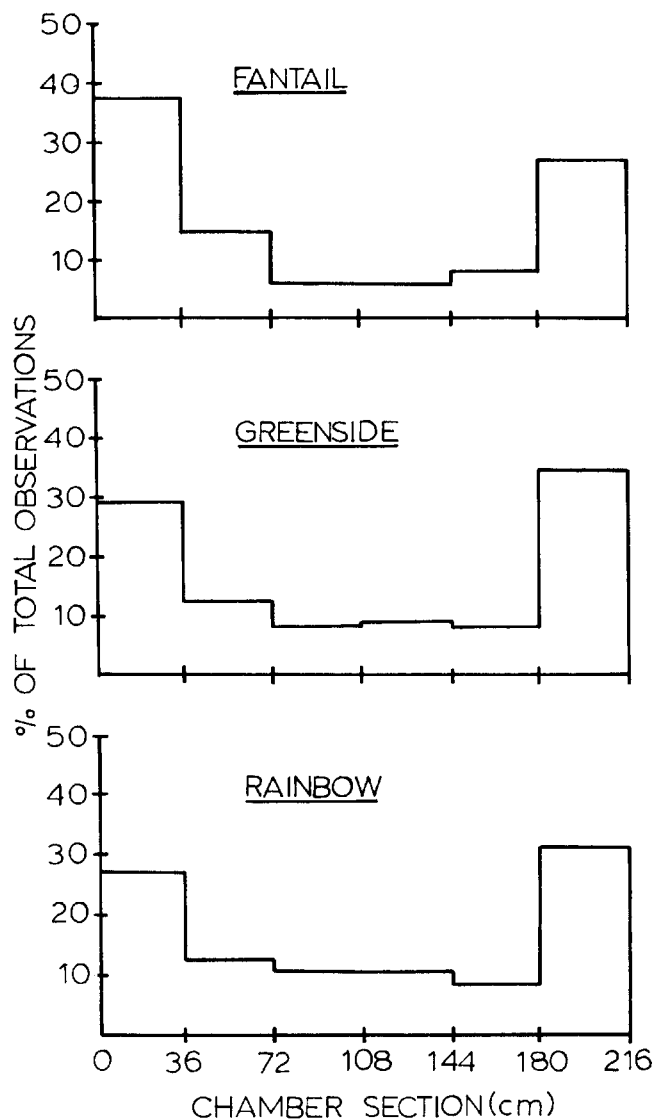


FIGURE 2. Typical control distributions of fantail, rainbow, and greenside darters in the test chambers in the absence of substrates. The six 36-cm sections of the chamber correspond to the following substrate size classes: 0-36 cm, sand; 36-72 cm, fine gravel; 72-108 cm, medium gravel; 108-144 cm, coarse gravel; 144-180 cm, pebble; 180-216 cm, cobble-boulder. The total number of observations for each species was 96.

of occurrence of the greenside darter on any of the other substrate classes never exceeded 14% in any season. Distributions on the substrates differed significantly ($P < 0.05$) from the control distributions for this species in all seasons. Although seasonal statistical differences in substrate use were observed, the greenside darter generally preferred the largest substrate classes.

When tested with the other two species, the greenside darter continued to exhibit a strong preference for the largest substrate classes in all seasons (Fig. 4). The percentage of observations on the two largest substrate classes ranged from 52.1% (spring) to 72.9% (summer). The mixed-species distributions of this species were significantly different ($P < 0.05$) from controls in all seasons, and also differed from the single-species test distributions in all seasons except autumn.

The rainbow darter demonstrated a low preference for the large substrate classes (Fig. 5). Use of the different

FANTAIL DARTER

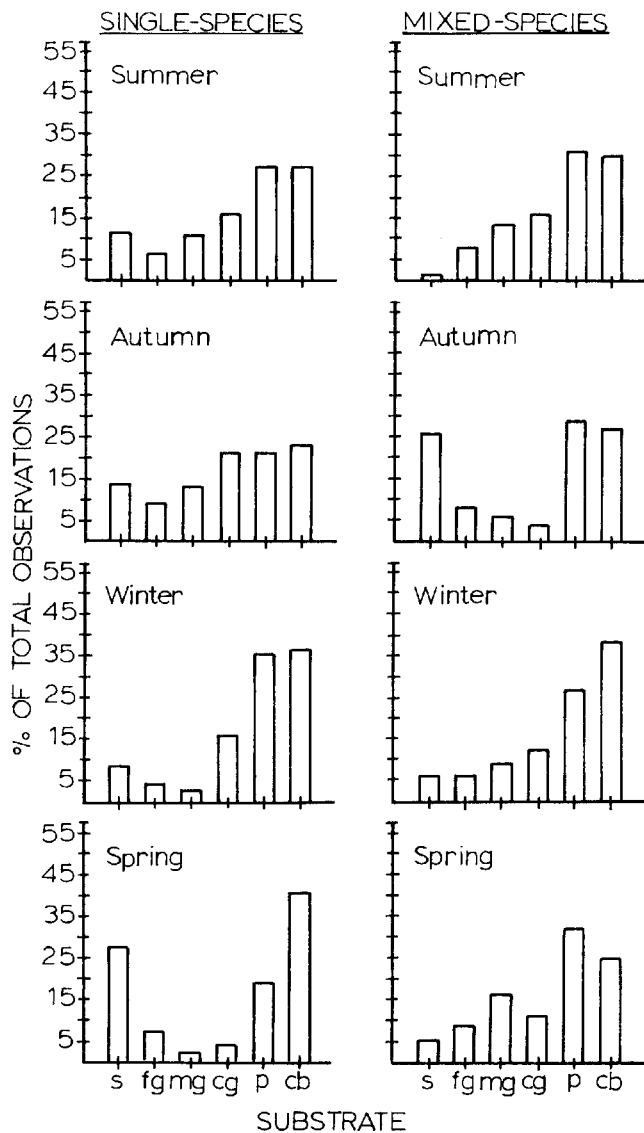


FIGURE 3. Distributions of fantail darters among substrate size classes in single-species and mixed-species tests. The total number of observations for each test was 192. Substrate classes: s, sand; fg, fine gravel; mg, medium gravel; cg, coarse gravel; p, pebble; cb, cobble-boulder.

substrate classes by this species was very similar in all seasons except autumn. In autumn, and to a much lesser degree in spring, the rainbow darter showed an increased preference for the larger substrate classes. Distributions on the various substrates were significantly different ($P < 0.05$) from control distributions in all seasons. No significant differences were found between the summer and winter distributions or the summer and spring distributions of this species. The distributions for the other seasons differed significantly ($P < 0.05$), owing to the increased use of the largest substrates (i.e., pebble and cobble-boulder) by the fish in autumn, and also to differences in use of sand and medium gravel in winter and spring (Fig. 5).

In the presence of the other species, the rainbow darter showed a relatively even distribution on the substrates in

GREENSIDE DARTER

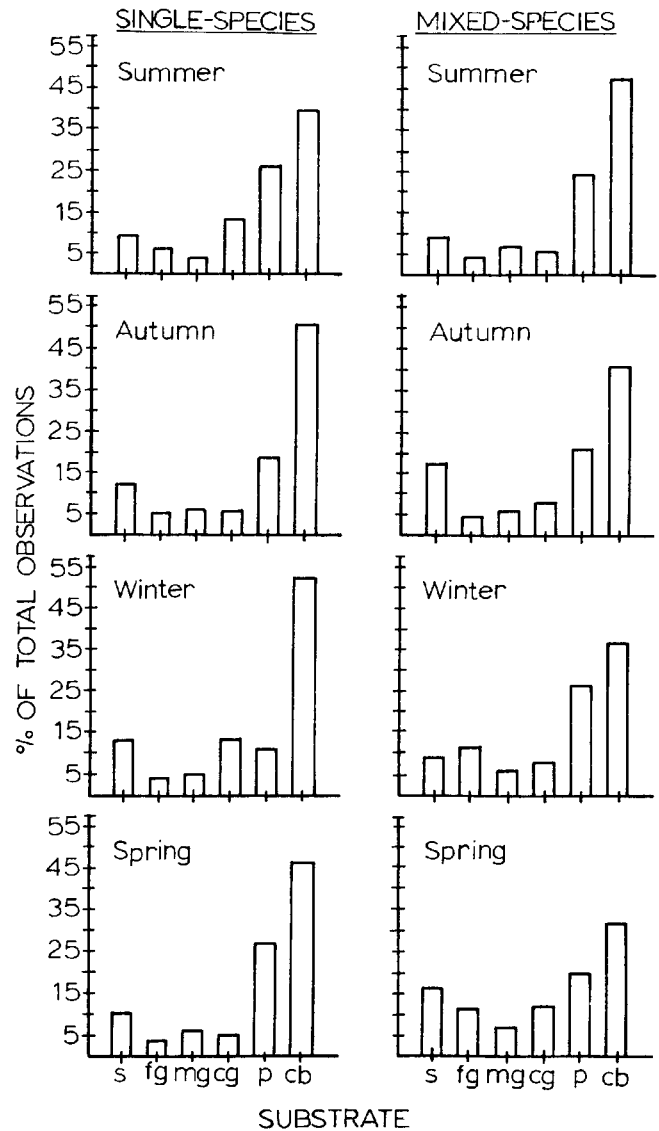


FIGURE 4. Distributions of greenside darters among substrate size classes in single-species and mixed-species tests. The total number of observations for each test was 192. Substrate classes: s, sand; fg, fine gravel; mg, medium gravel; cg, coarse gravel; p, pebble; cb, cobble-boulder.

all seasons except autumn, when the larger substrates were selected (Fig. 5). The distributions in all seasons were significantly different from the controls ($P < 0.05$). Seasonal distributions differed significantly ($P < 0.05$) only between autumn and spring. The rainbow darter, in the presence of congeners, was more evenly distributed on the substrates in spring than when tested alone. In both the single- and mixed-species tests, this species exhibited the lowest preference of the three species for the larger substrate classes. Its frequency of occurrence on the largest substrate classes ranged from 33.3% (summer) to 58.3% (autumn), when tested alone, and from 34.4% (spring) to 51.6% (autumn), when tested in the presence of the other two species.

In both the single-species and mixed-species tests, the majority (>50%) of greenside and rainbow darters oc-

RAINBOW DARTER

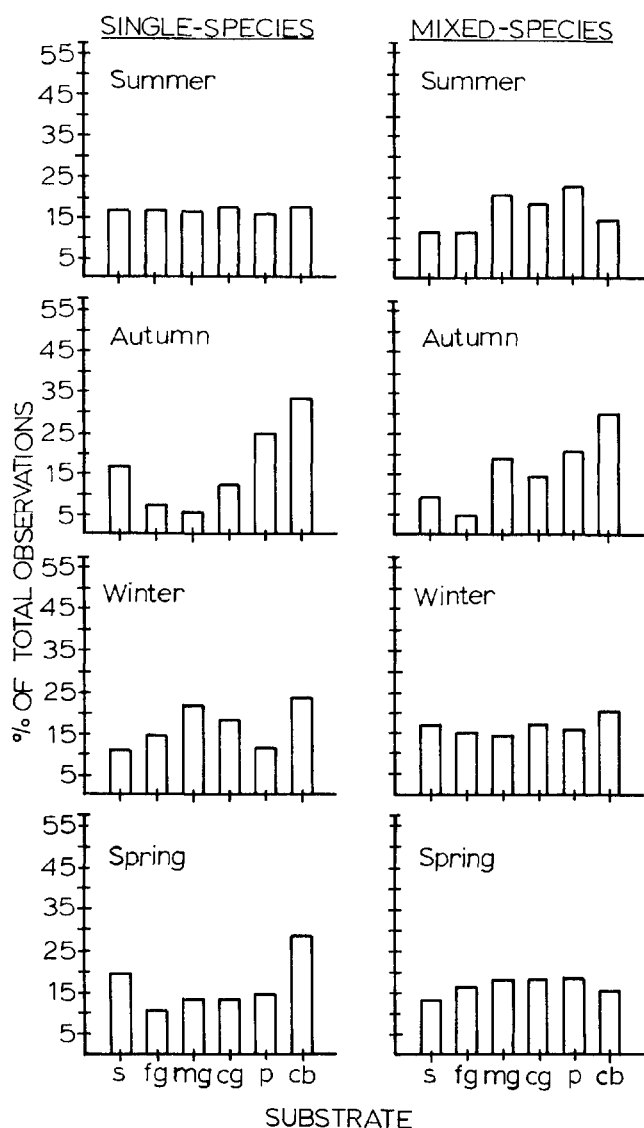


FIGURE 5. Distributions of rainbow darters among substrate size classes in single-species and mixed-species tests. The total number of observations for each test was 192. Substrate classes: s, sand; fg, fine gravel; mg, medium gravel; cg, coarse gravel; p, pebble; cb, cobble-boulder.

cupying pebble and cobble-boulder substrates were observed on the surface of these materials. In contrast, fantail darters were usually found under the largest substrates; few were observed resting on the surfaces of the substrates.

The results of the similarity analyses for the single-species tests revealed high levels of similarity (>0.600) in substrate-class use between the three species pairs in all seasons (Table 1). Similarity index values ranged from 0.643 (fantail \times rainbow darters in winter) to 0.875 (fantail \times greenside darters in summer). Similarities were greatest between fantail and greenside darters in all seasons except autumn. At that time, rainbow darters were very similar in their substrate preferences to both fantail (0.854) and greenside (0.812) darters. The lowest similarities observed in summer and spring occurred be-

tween greenside and rainbow darters, in autumn between fantail and greenside darters, and in winter between fantail and rainbow darters (Table 1).

In the mixed-species tests, the similarity indices for the species pairs remained high in all seasons (Table 1). The lowest values occurred between greenside and rainbow darters in the summer; in the other seasons, the lowest similarities were observed between fantail and rainbow darters. In summer, the highest similarity in substrate use was measured between fantail and rainbow darters; in autumn and winter the highest values occurred between fantail and greenside darters. No patterns of decreasing similarity were evident between the single-species and mixed-species results.

DISCUSSION

The different patterns of substrate use exhibited by rainbow darters in autumn and by fantail darters in autumn and spring may have reflected intra- and inter-specific territorial interactions between these species. Rainbow darters have been reported to seek deeper areas of riffles in late summer and autumn (Winn 1958a, Schlosser and Toth 1983). The largest substrates are generally found in the deepest areas of the riffle (Hynes 1970). In the present study, the increased number of occurrences of rainbow darters on pebble and cobble substrates in autumn may indicate selection by individual fish for the largest substrate particles. These particles may be used in turn as cues for finding deeper water in this season. The increased use of the largest substrates by rainbow darters in the autumn mixed-species tests may have resulted in displacement of some fantail darters from the pebble and cobble areas of the test chamber. Fantail darters observed on the sand substrate may have been displaced individuals seeking shelter in the corners of the chamber rather than individuals selecting the sand substrate.

Territoriality during the spring spawning season has been reported for fantail darters (Winn 1958a). If fantail darters tested in the spring were establishing territories in the chamber, some individuals may have been excluded from the larger substrates. Those individuals observed on sand may again have been merely seeking shelter in the corners of the test chamber. The absence of an increased occurrence of fantail darters on the sand

TABLE 1

Similarity indices (Schoener 1968) for substrate use by fantail (ft), greenside (gs), and rainbow (rb) darters in single-species and mixed-species tests. Values exceeding 0.600 indicate high overlap.

Season	Species Pairs		
	ft \times gs	ft \times rb	gs \times rb
<i>Single-Species:</i>			
Summer	0.8750	0.792	0.677
Autumn	0.7470	0.854	0.812
Winter	0.7423	0.643	0.683
Spring	0.8021	0.703	0.687
<i>Mixed-Species:</i>			
Summer	0.745	0.766	0.646
Autumn	0.802	0.722	0.798
Winter	0.917	0.708	0.719
Spring	0.781	0.760	0.792

substrate during the spring mixed-species tests may have resulted from the disruption of territory establishment by the presence of the other species.

Several investigators have suggested that darters may partition the habitat along the substrate axis (Wehnes 1973, Page and Schemske 1978, Schlosser and Toth 1984). In the present study, fantail and greenside darters exhibited strong preferences for the large substrate classes (i.e., pebble and cobble-boulder), and preferred the larger substrate classes regardless of test conditions. In contrast, the rainbow darter was less selective in its substrate preferences. This species, when tested alone or in the presence of the other two species, used all of the substrate types. If interspecific interactions are important in determining darter distributions within substrate classes, shifts in substrate use and decreases in the overlap values should have been observed, when substrate preferences were determined in the mixed-species tests. However, few shifts in substrate use occurred, and overlap values remained high. These results suggest that fantail and greenside darters may be more susceptible to interspecific interactions because of their similar substrate preferences.

Interspecific interactions between fantail and greenside darters may be reduced by differences in how the largest substrates are used by these species. For example, during the single-species tests, fantail darters occupying the pebble and cobble-boulder substrates were usually observed only by overturning these substrates. Few fantail darters (<50%) were observed at rest on the substrate surfaces. In contrast, the majority (>50%) of the greenside darters observed in the larger substrate classes were found on the surfaces of the substrates.

Although fantail, rainbow, and greenside darters can occupy different habitats within riffles (Lachner et al. 1950, Englert and Seghers 1983), they can also be collected in the same habitat in many streams (I. Hlohowskyj, pers. obs.). Competition for physical space and food resources may be high in riffles. The diets of fantail, rainbow, and greenside darters are very similar, with the three species feeding heavily on aquatic insect larvae (Adamson and Wissing 1977, Wynes and Wissing 1982, Hlohowskyj and White 1983). These species may reduce competition for food and space through differences in foraging area and foraging methods (Page and Swafford 1984). Because the fantail darter feeds primarily on aquatic insect larvae that occur in crevices between and beneath large substrate particles (Wehnes 1973, Schlosser and Toth 1984), the ability of this species to forage in these areas is, in part, governed by its morphology. Schlosser and Toth (1984) suggested that the fantail darter can use crevices in large substrates because it possesses a body that is flexible, partly because of the presence of very small scales. Page and Swafford (1984) concluded that a slender, flexible body and a terminal, oblique mouth are adaptations for living and foraging in crevices. Therefore, the presence for the large substrate classes exhibited by the fantail darter may have reflected the foraging niche of this species.

On the other hand, the greenside darter is strongly associated with aquatic plants (primarily *Cladophora* sp. and *Fontinalis* sp.) and feeds on insect larvae that live in this vegetation (Forbes and Richardson 1920, Fahy

1954, Wehnes 1973, McCormick and Aspinwall 1983). This species also uses attached filamentous algae for its spawning sites (Winn 1958a). Thick growths of *Cladophora* sp. and *Fontinalis* sp. are generally restricted to larger substrates that serve as stable attachment sites for the algae (Hynes 1970). The preference for the larger substrate classes exhibited by the greenside darter in the present study may indicate selection for large particles that secondarily can support attached forms such as epilithic algae.

Certain morphological characteristics of the greenside darter may also allow effective foraging on large, algae-covered substrates, and may be important in reducing interactions with fantail darters. The presence of a subterminal mouth would restrict the greenside darter to foraging on the surfaces of substrates (Page and Swafford 1984). The large body size of the greenside darter may also restrict access by this species to only the largest crevices between and beneath large substrates. Morphological differences could thus reduce competition for food between greenside and fantail darters when, as was evident in the present study, both species occupy the same substrate.

In the present study, the rainbow darter showed no strong preference for any single substrate type. The broad use of the various substrate classes by this species may be related to its morphology and method of foraging. The rainbow darter feeds on aquatic insect larvae taken from the surfaces of the substrate, rather than from crevices (Wehnes 1973, Schlosser and Toth 1984). It also has a subterminal, horizontal mouth adapted for foraging on substrate surfaces (Page 1983). Surface foraging by this species could result in competition with the greenside darter for food. However, the smaller body and fin sizes of the rainbow darter may restrict this form to slower portions of the riffle. This species has been reported to prefer the slower, more shallow portions of riffles (Winn 1958b, Wehnes 1973, Englert and Seghers 1983). The restriction of the rainbow darter to slower portions of the stream would act to decrease interactions with the greenside darter. The small size of the rainbow darter also suggests that this species could potentially forage within the smaller crevices of large substrates. Because these areas are similar to those used by the fantail darter, there is a potential for competition between these species as they forage for food. Schlosser and Toth (1984) have suggested, however, that owing to its larger scales and deeper, more rigid body the rainbow darter is incapable of exploiting the crevice microhabitats used by the fantail darter in large substrates. During the present study, rainbow darters occupying the larger substrates were found more frequently on the surfaces of the substrate, in contrast to fantail darters, which were hidden in the crevices. These observations are in agreement with Schlosser and Toth (1984).

The results of other studies indicate that current velocity and water depth may also be important in determining substrate partitioning by the darters (e.g., Lachner et al. 1950, Fahy 1954, Englert and Seghers 1983). Wehnes (1973) found that, although fantail and greenside darters preferred large substrate sizes, these species reduced interspecific interaction by partitioning the large substrates on the basis of water depth and

current speed. The greenside darter occupied large substrates in deep, fast water; the fantail darter used large substrates in shallower, slower waters. Although the effects of current velocity and water depth were not examined in the present study, it is clear that these factors may interact with substrate type and distribution to lessen competitive interactions among darters in the riffle environment.

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